OBSERVATIONS ON THE AUSTRALIAN ORNITHOPOD DINOSAUR, *MUTTABURRASAURUS*

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New material and a restudy of old suggests that *Muttaburrasaurus* is not an iguanodontid ornithopod, but probably diverged from the iguanodontian-hadrosaur lineage prior to the divergence of taxa such as *Dryosaurus* and *Tenontosaurus*. The type skull differs from a second, older skull from the Allaru Mudstone in ways that suggest a trend toward the evolution of a continuous more-or-less planar sheet of enamel along the labial face of the maxillary dentition. Teeth from Lightning Ridge (Griman Creek Fm.) may pertain to a more plesiomorphic species of *Muttaburrasaurus*. □ *Muttaburrasaurus, Ornithopoda, Australia.*

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The discovery of a new skull of *Muttaburrasaurus* (from 'Dunluce', north-central Queensland) and further preparation of the holotype skull has yielded interesting new information bearing on its evolution and systematic position. Because preparation of both skulls proved more difficult and hence slower than expected, it is worthwhile presenting interim results that substantially alter the phylogenetic interpretation of Bartholomai & Molnar (1981) and Molnar (1984). New information on cranial features, especially those relevant to understanding the phylogenetic position of *Muttaburrasaurus* in relation to the classification presented by Sereno (1986), are given here. Some remarks on postcranial features are also included.

Collection designations. AM, Australian Museum, Sydney; NMV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane.

DESCRIPTION

HOLOTYPE SKULL (QM F6140). The original description of the skull of *Muttaburrasaurus langdoni* included no description of palatal or braincase structure and these are described here, insofar as feasible with the still incomplete state of preparation. Comments on the maxilla, the postorbital bar and the general form of the skull follow.

Quadrate. The quadrate is a robust columnar element, similar to those of other advanced ornithopods. The articular end remains in articulation with the mandible, and so cannot be examined in detail. The body is straight in lateral view as in *Iguanodon bernissartensis*, not curved as in *I. atherfieldensis*. The posterior surface, inclined to face slightly medially, tapers upwards to become a sharp ridge formed by the meeting of the lateral and medial surfaces of the element. A broad pterygoid wing projects anteromedially to meet the pterygoid in a smooth curve (Fig. 1). Posteriorly this process bears a marked concavity, adjacent to a vertical sulcus on the upper part of the body of the bone. The lateral face (jugal wing) projects anteriorly beneath the quadratojugal and is embayed by the round margin of the quadrate foramen.

Exoccipital. Presumably the exoccipitals and opisthotics are fused, but only the exoccipital portion of the compound element is easily visible, to best advantage on the left side. A dorsoventrally deep paroccipital process extends posterolaterally from the condyar region. Although the distal end is lacking, there is no indication that the process was declined distally as in *Iguanodon* and hadrosaurids (Fig. 2).

Medially a stout pillar descends from the paroccipital process to abut on the basioccipital and form the dorsolateral part of the occipital condyle. Part of the condyle, separated by a shallow groove from the ventral moiety, may be made up by the exoccpital. Because the contacts are fused it isn't clear that this is actually part of the exoccipital, as there is another possible contact — a discontinuity in the surface grain of the bone — at the junction of the pillar and the base of the paroccipital process. Just anterior to the presumed junction, there is an anteroposteriorly-directed concavity. This has yet to be fully cleaned but is likely to accommodate foramina for cranial nerves X, XI and XII.

Basioccipital. Only two points may be added to the original description. The articular surface of the condyle extends forward to form a lip

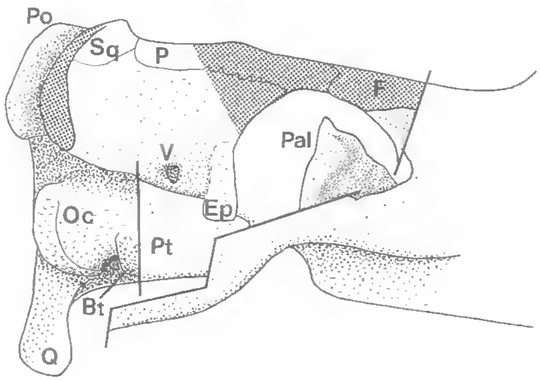

FIG. 1. Cutaway interpretation of braincase and posterior palatal structures of *Muttaburrasaurus langdoni*, QM F6140. Bars indicate cuts through the jugal arch, prefrontal region and quadrate wing of pterygoid. Dots indicate broken bone surfaces. Bt=basal tubera (basisphenoid), Ep=epipterygoid, F=frontal, Oc=occipital condyle, P=parietal, Pal=palatine, Po=paroccipital process, Pt=pterygoid (quadrate wing), Q=quadrate, Sq=squamosal, V=presumed trigeminal foramen.

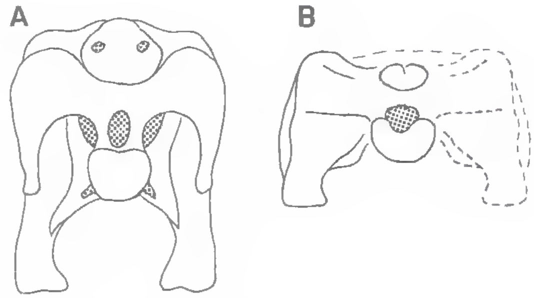

FIG. 2. Skulls of A, *Iguanodon bernissartensis*; and B, *Muttaburrasaurus langdoni* in occipital view, to show the difference in forms of the paroccipital processes. To scale. (A redrawn from Norman, 1980, and B from Bartholomai & Molnar, 1980.)

'overhanging' the neck of the condyle, so the surface describes an arc in excess of 180° as in *I. atherfieldensis* (Norman, 1986, fig. 18). This lip connects with the basal tubera by a low, blunt keel on the ventral face of the condylar neck.

Basisphenoid. Only the inferior, and some of the lateral, surface of the basisphenoid is clearly visible and it carries large basal tubera, confluent medially to form a rugose transverse ridge. The left tuber is deflected sharply posteriorly and the right is incomplete. A large foramen on each side penetrates the tubera at the junction with the keel connecting to the occipital condyle. On the midline the ventral face of the confluent tubera has a larger foramen (Fig. 3). This foramen is in the same relative position as that of the median eustachian foramen (f. intertympanicum) of modern crocodilians, but whether or not it represents that structure cannot be determined at present.

About 2cm in front of the tubera, two robust 4cm-long basipterygoid processes extend ventrolaterally and somewhat anteriorly to contact the pterygoids. Just anterior to the tuber on the left side, a sheet of bone curls out from the basisphenoid (or prootic?) joining it to the quadrate process of the pterygoid. Although so far only partly prepared this seems to be very similar to a character state used to diagnose the Pachycephalosauria: Prootic-basisphenoid plate present which extends laterally from the braincase, contacting the pterygoquadrate wing and effectively separating subtemporal and occipital regions (Sereno, 1986). In *Muttaburrasaurus* this contact also separates the subtemporal (adductor) chamber from the occipital region.

Pterygoid. Both right and left pterygoids are preserved, but that of the right is visible only in the basipterygoid-quadrate region, and that of the left is fragmentary. The quadrate process is a vertical sheet, with an acutely angled posterior margin, projecting posteriorly from the basipterygoid contact and laying ventral to the pterygoid wing of the quadrate ('Pt' in Fig. 1, where the entire extent is not shown). It bears a broad, blunt median longitudinal ridge. Anteroventrally it contacts another sheet laying in a plane inclined at about 45° to the horizontal. The extent of this portion cannot be determined without further preparation. The basipterygoid joint, which seems to have been immobile, is just anterior to the contact between these two sheets. In front of the joint a tapered process of the pterygoid extends medially and curves through 180° to form a (more or less) horizontal hook-like structure (Fig. 3, 'mp').

Epipterygoid. A few fragmentary sheets of much abraded bone between the laterosphenoid and the pterygoid on the right side probably represent the epipterygoid. They show little other than that one was present in the usual position (Fig. 1, 'Ep').

Palatine. The right palatine is visible and somewhat worn. It seems to be a thick, triangular plate rising sharply from the maxilla, with its dorsal margin just below or contacting the prefrontal (Fig. 1).

Maxilla. In QM F6140 the maxillae are orientated so that their toothrows have been brought

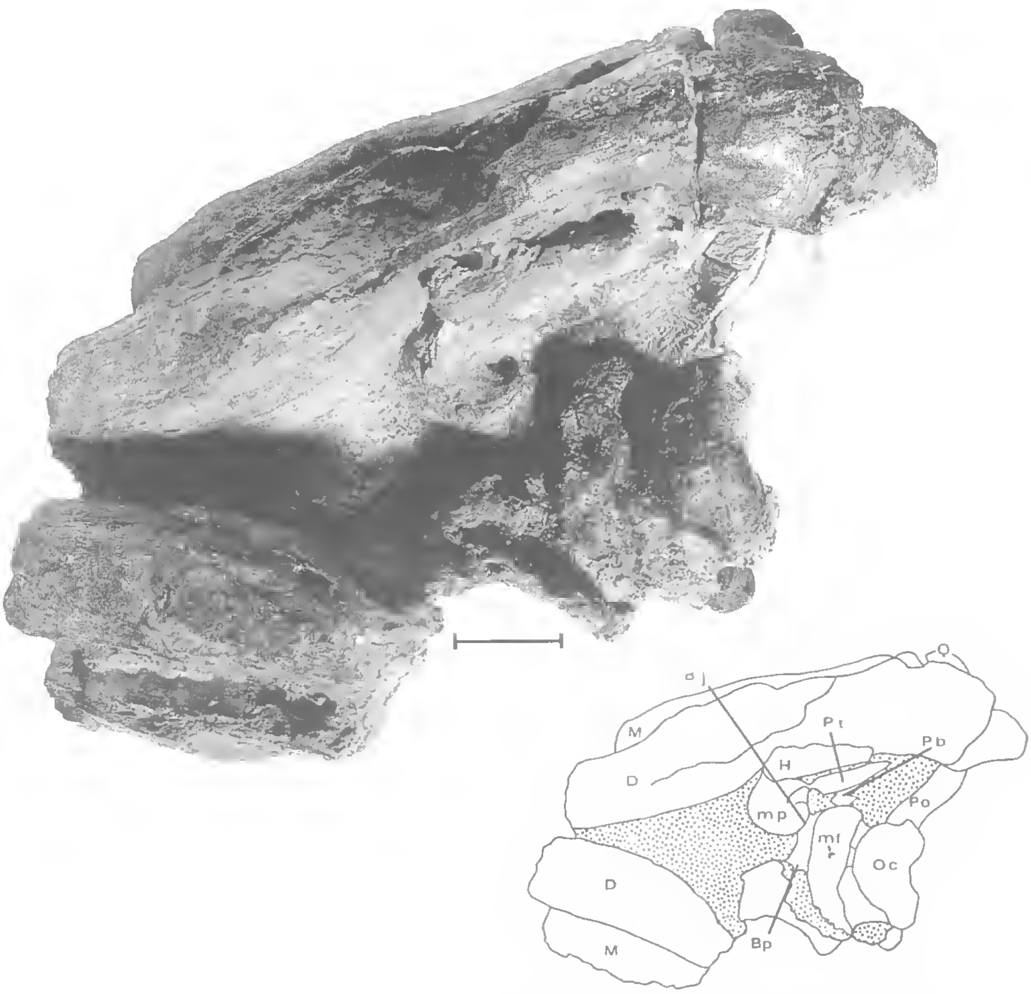

FIG. 3. The skull of *Muttaburrasaurus langdoni*, QM F6140, in ventral view. Bj=basipterygoid joint, Bp=basipterygoid process (basisphenoid), D=dentary, H=hyoid piece, M=maxilla, mf=median ventral foramen of basisphenoid, mp=medial hooked process of pterygoid, Pb=pterygoid-braincase contact. Other abbreviations as in Fig. 1. Scale = 50mm.

together, with the crowns only 5cm apart, directed toward one another with the labial faces of the teeth facing ventrally. The maxillary toothrows of the 'Dunluce' skull (QM F14921) have also been brought together, about 3cm apart, by crushing. The orientation of the maxillae in this specimen suggests that those of the holotype have been folded underneath the skull, so that their lateral surfaces have come to face ventrally. In fact this has also happened to a lesser extent in the 'Dunluce' skull, as shown by fracturing of the posterior part of the right maxilla. Such fractures are not apparent in the type skull, which has either suffered plastic deformation or rotation of the maxillae about their dorsal margins. Since such rotation has been proposed as a masticatory device in the iguanodontian-hadrosaurian lineage (e.g., Weishampel, 1984; Norman & Weishampel, 1985), it is interesting to see if it was present in *Muttaburrasaurus*. The lateral surface of the posterior part of the left maxilla of the type skull curves through a 90° arc (in the frontal plane) beneath the orbit, from the nearly horizontal surface adjoining the jugal to the nearly vertical surface at the alveoli. But just forward of this the alveolar region has been flexed so that the teeth become directed medially, as described above. This suggests that this maxilla at least is

deformed, and provides no evidence for (or against) flexure at the maxillary-nasal junction. The reconstruction of the type skull (Fig. 4) corrects for this distortion.

Postorbital bar. Unlike the condition of most other ornithopods the postorbital bar of *M. langdoni* is more extensive transversely than anteroposteriorly (Fig. 5). In other words, it is broad. The descending process of the postorbital is 4cm wide (transversely) but only 1.75cm in the longitudinal dimension. The ascending process of the jugal is similarly formed, so the postorbital bar partly divides the orbital cavity from the adductor chamber. A similar state, postorbital bar transversely broadened with an interdigitating postorbital-jugal suture, is used by Sereno (1986) to partly define the Goyocephalia, the node just distal to the Pachycephalosauria. The contact between the jugal and postorbital in *M. langdoni* is tight, but only actually interdigitates at the tip of the ascending process of the jugal.

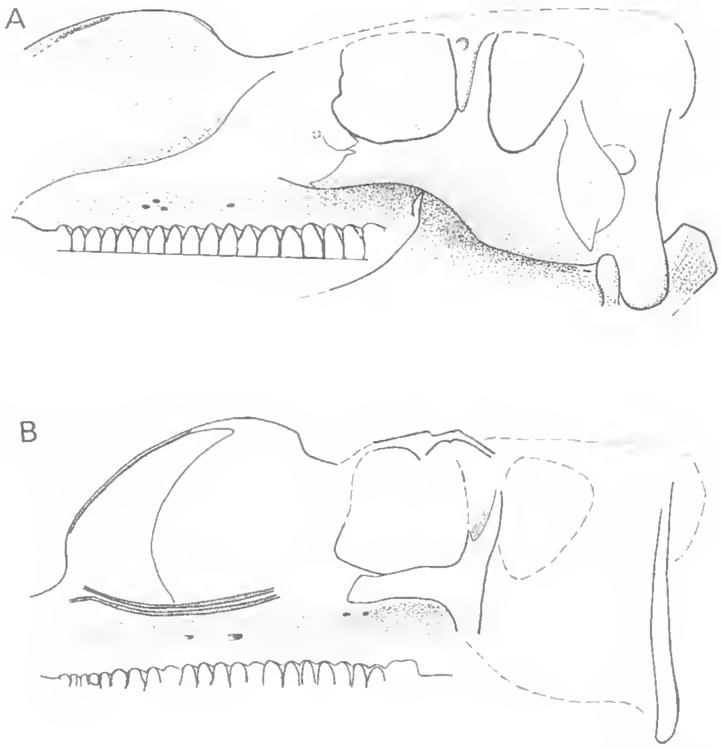

FIG. 4. Reconstruction of skulls of A, *Muttaburrasaurus langdoni* (QM F6140); and B, *Muttaburrasaurus* sp. (QM F14921). Restored portions in dashed lines. The region of the jugal and of the junction between the nasal bulla and body of the maxilla in QM F14921 is worn and hence the structures shown (form of jugal-maxillary contact and clefts beneath bulla) may represent structures just below the surface of the skull. The last maxillary tooth is very poorly preserved, so it is not certain if the last alveolus as drawn represents a single alveolus or two.

Skull form. Molnar (1995) presented an argument, based on the type skull, that the postorbital region was enlarged relative to those of other ornithopods. This may be seen in Fig. 6, and has directed the orbits very slightly to the front. Although dorsoventrally deep, the snout was seemingly relatively narrow. The 'Dunluce' skull, in spite of its crushing, confirms that the postorbital region was approximately twice as broad as the snout.

'DUNLUCE' SKULL (QM F14921). The second skull was collected by Dr Mary Wade in 1987 from the Allaru Mudstone (not the Toolebuc Fm., as reported by Molnar, 1995) on Dunluce station, about halfway between Hughenden and Richmond in north-central Queensland. The Allaru Mudstone, a gray calcareous marine argillite, underlays the Mackunda Fm. from which the holotype derives. Thus this second specimen derives from an older population (although still Albian) than the type. The skull is probably more complete that the holotype skull but has been laterally sheared and crushed, so that the the nasal bulla has been flattened and the skull roof has come to lie almost coplanar with the right side (Fig. 7). The postorbital region is severely damaged on the left, so that the quadrate now rests in the position of the posterior orbital margin (Fig. 7A). The postorbital is missing entirely on this side, and the (empty) impression for its reception may be seen on the ascending process of the jugal. Because of the damage, and because preparation is still in a preliminary stage, a full description of this skull will not be given here. Instead selected relevant features are reported. This skull is identified as *Muttaburrasaurus* on the basis of its general form, as well as the apomorphic nasal bulla and tooth form. Because of the damage and incomplete preparation, as

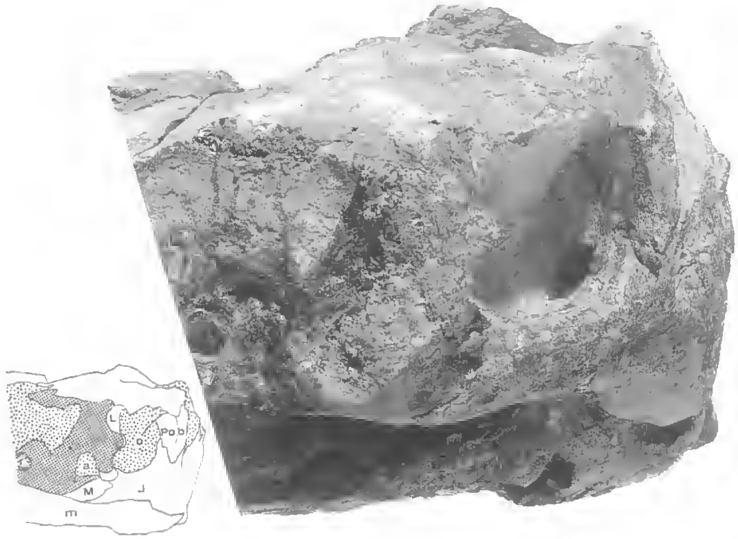

FIG. 5. The skull of *Muttaburrasaurus langdoni* (QM F6140) in anterolateral view, showing the breadth of the postorbital bar (Pob). Dots indicate broken bone surface; open dots indicate matrix. m=mandible, J=jugal, o=orbit, a=antorbital fossa, r=root of maxillary tooth, L= lachrymal. Other abbreviations as in Fig. 3.

well as the possession of partly erupted maxillary crowns anteriorly in the toothrow (those of *M. langdoni* are completely erupted along the entire visible maxillary toothrow) and differences in form, it is premature to assign it to *M. langdoni*, and it is referred to *Muttaburrasaurus* sp.

Nasal bulla. The anterior termination of nasal bulla is not preserved on the type skull, but on QM F14921 it seems to be present. Although much of the bony surface of this specimen has been lost surface bone is present at the front margin of the nasal bulla. Here the surface forms an anteriorly-directed vertical face, which then presumably bends through a right angle — the flexure itself is still embedded in carbonate — to give an adjacent horizontal bone surface extending anteriorly to the break at the front of the specimen. Although the nasal bulla has been flattened during preservation, it seems unlikely such transverse compression could create an illusory anterior termination to the bulla. This observation has been incorporated into the new reconstruction of the skull in Fig. 4B.

Although the nasal bulla of QM F4921 is badly crushed and incompletely prepared, some features can be better seen than in the holotype. On the right side, a crescentic element makes up the anterodorsal part of the lateral wall of the bulla (Fig. 7B). The left is worn and incompletely prepared and so difficult to interpret, but gives no reason to doubt or modify the interpretation here given. This element contacts that, presumably the nasal, making up the dorsal roof of the bulla posteriorly, and what seem to be slit-like nares anteriorly. The concave inferior margin of the bone is unbroken, so that the posteroventral part of the lateral wall must have been formed by another element, not preserved. Thus the cresecentic element may be, or be part of, the premaxilla. This element cannot be seen on the bulla of the type skull, where instead the lateral wall seems to be made up of a single element. There is no clear indication of narial openings on such of the maxillae as is preserved anterior to the bulla.

Ventrally the bulla seems to have been separated from the underlying maxilla by two clefts, separated from each other by a thin sheet of bone (Fig. 7A). This sheet is continuous with the maxilla anteriorly, so the lower of the clefts seems to be part of the maxilla. These structures are also apparent on the left side, but cannot be seen in the type skull, presumably because they are internal structures exposed by wear on the 'Dunluce' skull. A thin median septum is apparent within the bulla, as in the type skull (which also has a second vertical sheet, described in Molnar [1984] more laterally placed at the left edge of the left narial opening). The bulla of the type skull also shows on its badly worn left side one, or perhaps two, thin, seemingly horizontal internal sheets of bone.

Antorbital fossa. The apparent antorbital fenestra on the left side of the 'Dunluce' skull (Fig. 7) is entirely surrounded by abraded bone that had been exposed prior to discovery. This has exposed a triangular antorbital fossa of respectable size, approximately 5 x 7cm.

Tooth replacement. The holotype skull is unusual among ornithopods, as well as other reptiles, in that there is no indication of the sequence of tooth replacement in the maxillary dentition. In fact, replacement teeth can be seen only where the skull has been broken transversely behind the nasal bulla. (The dentary crowns now visible

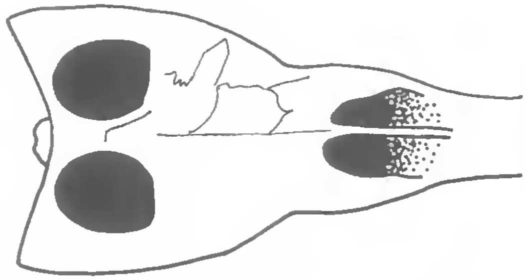

FIG. 6. Reconstructed skull of *Muttaburrasaurus langdoni* (QM F6140) in dorsal view. (From Molnar, 1995.)

seem to show an alternating pattern of replacement.) The 'Dunluce' skull has a complete, or almost complete but bady weathered, right maxillary toothrow. There are 22 tooth positions, with what seem to be replacement crowns in positions 4 and 6 (from the front). Only 15 positions are visible in the type skull, probably 6 to 21 assuming that it, too, had 22 maxillary teeth, and the anterior-most teeth are not well preserved. Thus some replacement in the type skull cannot completely be ruled out, but there is no indication of it.

TEETH

Maxillary teeth. Only the maxillary teeth of *M. langdoni* were described by Bartholomai & Molnar (1981). Although 17 maxillary crowns are exposed on the left side of the type skull, only three preserve substantial portions of the lateral face. These crowns differ from those of all other ornithischians in that they show an almost flat (slightly convex) lateral face marked by a series of parallel ridges and grooves, all of which are equally developed (Fig. 8). The ridges extend to the base of the crown anteriorly (mesially) but become progressively shorter posteriorly. They — with one possible exception — do not converge. None of the crowns shows clear indication of a primary ridge. On two, however, a primary ridge adjacent to the posterior (distal) margin of the crown is evident. This presumed ridge is only marked as such by an adjacent sulcus along the posterior margin (this sulcus is the 'deep groove' of Bartholomai & Molnar, 1981). Each crown slightly overlaps that posterior to it.

Maxillary crowns are also known in the 'Dunluce' skull, QM F14921, and probably — as isolated teeth — from Lightning Ridge. The latter were held in the private collection of Ms Elizabeth Smith but have been donated to the Australian Museum, and represented by casts in the Queensland Museum. As mentioned previously, most of the exposed maxillary crowns of the 'Dunluce' skull are poorly preserved, with their lateral faces badly weathered, but a fortuitous break on the left side exposed a well-preserved crown near the posterior end of the toothrow (Fig. 8B, E), probably number 19 or 20. The ornament of this crown is like that of the the type skull, but differs in some notable ways. The lateral face is almost flat, slightly concave, and bears 11 low ridges. These ridges are relatively larger than those of the holotype skull and broader, with flat — in some cases slightly grooved — tops. Most apparent, however, is the clear primary ridge near the distal margin with 8 of the low ridges mesial to it and 3 distal. In some ways this crown more closely resembles those of *Atlascopcosaurus loadsi* (NMV P157390) than those of the holotype skull. However, the maxillary crowns of QM F14921 do resemble those of the holotype in: outline of the crown; almost flat lateral face; large number of low, parallel grooves and ridges; and a low primary ridge near the distal margin.

The teeth from Lightning Ridge (New South Wales) from the Smith collection include one worn specimen preserving the root and base of the crown (QM F14420 [cast]), and a second that is almost complete (QM F14421 [cast]). (A third tooth, AM F81865, may also pertain to *Muttaburrasaurus*). They derive from the Griman Creek Fm. at McNamara's Three-Mile Field and were collected in, or just before, 1986. These were previously noted, but not described, by Molnar & Galton (1986). The first is too incomplete for consideration here — and may derive from the dentary — but the second shows a crown basically similar to that of the 'Dunluce' skull (Fig. 8F). It has a series of 6 low, parallel ridges mesial to a primary ridge, fewer than in QM F14921, and 1-2 distal to it in a shallow sulcus. It is also smaller than the 'Dunluce' tooth, about 69% as wide. The crown is referred to *Muttaburrasaurus*, rather than *Atlascopcosaurus*, on two character states: a curved (not angulate) proximal margin to the crown; and the extension of the primary ridge to the base of the lateral face. In *A. loadsi* the primary ridge extends to the distal margin of the crown rather than the proximal, and there is no real proximal margin, rather the mesial and distal margins converge (Fig. 8G).

Unlike any of the crowns in either the type or 'Dunluce' skulls, this crown (QM F14421) shows the lingual surface, which bears a series of at least four parallel, shallow grooves. Unfortunately, due to the silicification of the specimen it is not possible to determine if the surface bore enamel

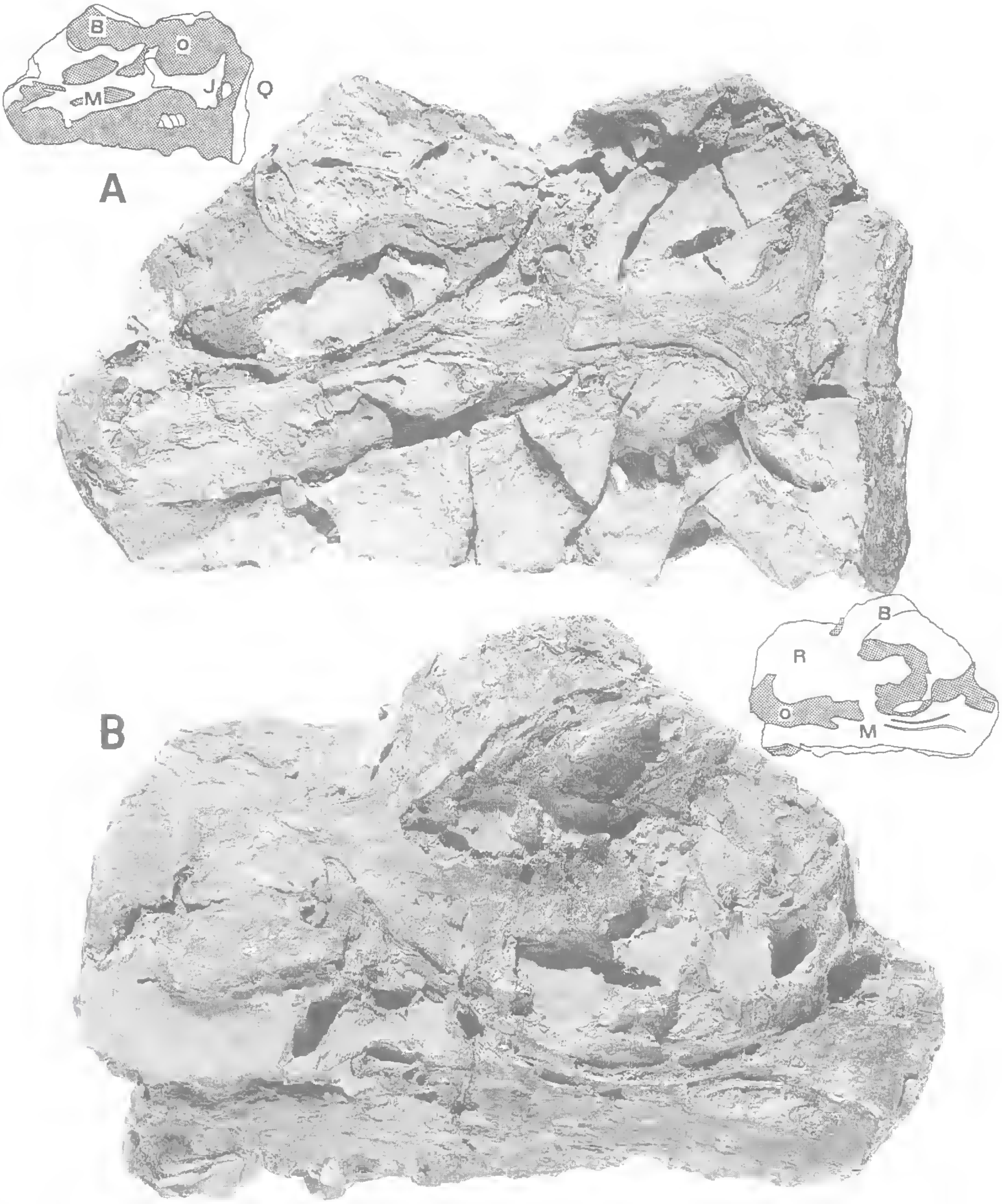

FIG. 7. The partially prepared skull of *Muttaburrasaurus* sp. (QM F14921), from the left A, and right B. The skull has been crushed, and the apparent antorbital fenestra and opening in the lower part of the nasal bulla are artefacts of erosion on the left side. The left quadrate has been displaced anteriorly to the region of the anterior margin of the laterotemporal fenestra.B=nasal bulla; R=skull roof.

and, if so, how much. The maxillary crowns of *A. loadsi* also have a series of shallow, parallel grooves on their lingual faces as does an incomplete crown referred to *Muttaburrasaurus* sp. from near Hughenden (QM F12541) (Fig. 8C).

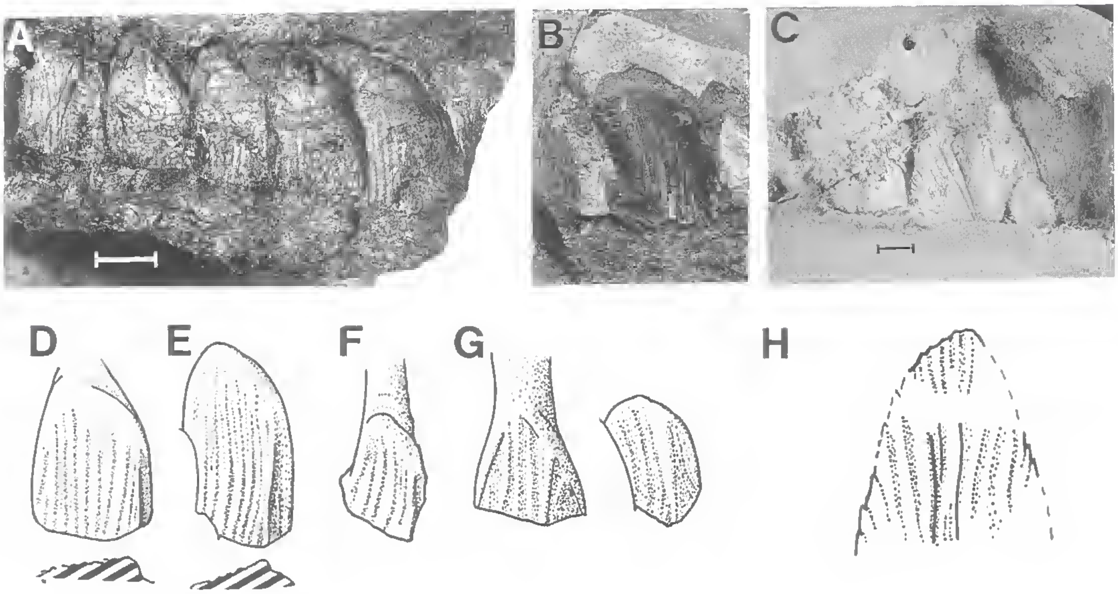

FIG. 8. Teeth of *Muttaburrasaurus*. A, Anterior maxillary teeth of *M. langdoni* (QM F6140). B, Posterior maxillary crown of *M.* sp. (QM F14921). C, Dentary crowns of *M.* sp. (QM F12541). D,, Right 11th or 12th maxillary crown of *M. langdoni* (QM F6140). Section through crown at bottom, showing position of presumed primary ridge. E, Left posterior maxillary crown of *M.* sp. (QM F14921). Section through crown, as in E, at bottom. F, Maxillary crown of *M.* sp. (QM F14421). G, Two maxillary crowns of *Atlascopcosaurus loadsi* (NMV 157390).H, Reconstructed dentary crown of *Muttaburrasaurus*, based on QM F12541 and QM F6140.

Dentary teeth. Dentary crowns have been exposed on the type skull, and also occur in a very fragmentary specimen (QM F12541) from the Allaru Mudstone from 'Iona', southeast of Hughenden. This was tentatively referred by Molnar (1984) to 'an unusually large hypsilophodont' on the basis of what are now recognised as plesiomorphic ornithopod or even euornithopod character states. This specimen is part of an associated partial skeleton, which has remained in Hughenden. It consists of parts of two dentary crowns found in a small block of carbonate, together with natural molds of parts of four other teeth. One of these represents the lingual face of the maxillary tooth mentioned above.

No dentary crown is completely exposed in either specimen, so only the upper half (or a little more) toward the tip may be described. The crown seems to be rounded, perhaps leaf-shaped, in form. A prominent carina occupies the middle, with a series of lower, parallel ridges, varying in size, occupying the face mesial and distal to it (Fig. 8C, H). These ridges are inclined to the carina and terminate at the margin in small, tapering denticles. The denticles are featureless, except that some divide distally, so that one ridge may bear two denticles. In at least one specimen (QM F12541) the carina itself bears four or five low, parallel ridges basally. In all discernible features the dentary crowns of the type skull match that of QM F12541. A single displaced dentary tooth of the 'Dunluce' skull is also indistinguishable from these.

POSTCRANIUM (HOLOTYPE)

Manus. Initially *Muttaburrasaurus* was believed to be an iguanodontian, closely related to *Camptosaurus* (Bartholomai & Molnar, 1981): this work was carried out before the influence of phylogenetic systematics was felt in ornithischian taxonomy. At that time an incomplete flattened, tapering element was thought perhaps to represent a thumb-spike. If *Muttaburrasaurus* is indeed an ankylopollexian, this is a plausible interpretation. However, the bone is poorly preserved, abraded and broken. Therefore — in the absence of any assurance that *Muttaburrasaurus* is in this lineage and is as or more advanced than *Camptosaurus* — the piece cannot be reliably identified as a thumb-spike and so does not constitute evidence that *Muttaburrasaurus* is an ankylopollexian.

FIG. 9. Reconstruction of the skeleton of *Muttaburrasaurus langdoni* showing what parts are actually preserved. Scale = 1m.

Pes. During the reconstruction (Fig. 9) of *M. langdoni*, the pedal elements were re-examined. Further cleaning of the pieces revealed a contact between the proximal and distal parts of metatarsal III. This shows that the metatarsus is shorter than originally believed (Fig. 10), and reduces the anomalous disparity in length between metatarsal III and the others.

SYSTEMATIC POSITION

Since the original description of *Muttaburrasaurus* much new work on advanced ornithopods has appeared. The original interpretation of its systematic position was based significantly on Dodson (1980), but the re-interpretation of ornithischian phylogeny by Sereno (1986) suggests that a review of the position of *Muttaburrasaurus* is in order. Consideration of the original and new character states suggests that *Muttaburrasaurus* is not an iguanodontid (or camptosaurid), but a basal ornithopod whose lineage diverged early from the iguanodont-hadrosaur lineage.

Because of the incompleteness of the *Muttaburrasaurus* material (Fig. 9) many of the character states used by Sereno (1986) are not observable. The remaining states are assessed for *Muttaburrasaurus*, based on the type specimen but with some observations from the 'Dunluce' specimen. Three (mandibular dentition offset medially; moderate coronoid process; pubic peduncle of ilium less robust than ischial peduncle) of the seven states used by Sereno to diagnose the Genasauria are present in *Muttaburrasaurus*, so its inclusion in that group is reasonable.

States are considered in order of the nodes they define.

ORNITHOPODA

External opening of the antorbital fossa of moderate size or smaller: Present. The antorbital opening is present but small in the type skull. Unfortunately shedding of the surficial bone makes it impossible to tell just how small the opening was. The 'Dunluce' skull seems to have a relatively large antorbital opening for an ornithischian, however as mentioned previously this is an artefact arising from the loss of surficial bone. The type skull is fortuitously broken at the antorbital fenestra and shows that a relatively thin plate of bone laterally walls the antorbital fossa around the small antorbital opening.

The remaining three character states are not presently determinable, but the single state known gives no reason to doubt that *Muttaburrasaurus* is an ornithopod.

HYPSILOPHODONTIA

Prepubic process rod-shaped; wider transversely than tall dorsoventrally: Absent. The prepubic process in *Muttaburrasaurus* is mediolaterally compressed, taller than wide and not rod-shaped.

The other three character states are not determinable for *Muttaburrasaurus*, but the state here assessed gives no evidence for its being a hypsilophodontian.

IGUANODONTIA

Leaf-shaped denticles: Absent. Although denticles are present on the dentary teeth they are tapered in form, not leaf-shaped (Fig. 8C, D). The maxillary crowns do not (observably) have denticles.

Strong primary ridge on medial surface of dentary crowns: Present (Fig. 8C, D). Strong primary ridges are present on the dentary crowns in the type and 'Dunluce' skulls, and QM F12541.

External opening of the antorbital fossa is relatively small or entirely absent: Present, as mentioned above, in the type skull.

Quadratojugal reduced in size relative to the quadrate: Absent. As may be seen from Fig. 4A (and fig. 2, Bartholomai & Molnar, 1981) the quadratojugal is about as large (in its lateral extent) as the quadrate, maybe larger. It is not reduced relative to the quadrate.

Femur with weak anterior intercondylar groove and deep posterior intercondylar groove: Absent. The femur does indeed have a deep posterior intercondylar groove (Fig. 11A), but the anterior intercondylar groove is deep as well (Fig. 11B).

The other nine character states are not presently determinable, but as only two of the five determined agree with Sereno's states for iguanodon-

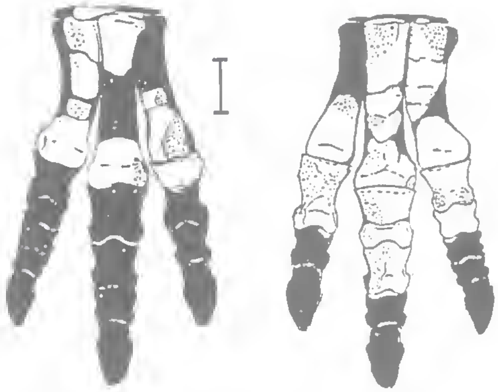

FIG. 10. Pes of *M. langdoni* (QM F6140) in dorsal (right) and plantal (left) views. Scale = 150mm.

tians, *Muttaburrasaurus* is probably not an iguanodontian.

DRYOMORPHA

Maxillary crown narrower anteroposteriorly than the opposing dentary crown: Present. The preservation of maxillary and dentary teeth in juxtaposition in the snout region of the type skull, shows that the maxillary crowns are indeed narrower than the dentary crowns, which overlap in their medial exposure. Overlap is less in the maxillary toothrow (Fig. 8A).

Lateral maxillary primary ridge stronger than the medial dentary primary ridge: Absent. Although there is a primary ridge on the maxillary crowns (not mentioned in Bartholomai & Molnar, 1981), this ridge is placed adjacent to the anterior (mesial) edge of the lateral face of the crown, and is less prominent than the corresponding ridge of the dentary crowns (Fig. 8A, B, E, F vs. C, D).

Diamond-shaped maxillary and dentary crowns; crowns with rounded anterior and posterior corners: Absent. As may be seen from Fig. 8, neither maxillary nor dentary crowns have diamond-shaped lateral faces, although in section they do exhibit rounded anterior and posterior margins (which is what I believe to be meant by 'anterior and posterior corners').

Space separating ventral margin of quadratojugal from jaw articulation: Present, in the type skull (Fig. 4A).

Ischial shaft round in cross section; transversely compressed distally: Absent. Only the proximal portions of both ischia are preserved so the presence of distal compression cannot be verified. However, the proximal parts of the shaft are compressed not round in section.

Two (or two and a half) of the five determinable character states (out of a total of eight) for dryomorphs can be found in *Muttaburrasaurus*. In view of the lack of match with the character states for more basal nodes it seems likely that *Muttaburrasaurus* is not a dryomorph, but the states that can be assessed are equivocal.

ANKYLOPOLLEXIA

Close packing along the toothrow and in the replacement series eliminating spaces between the bases of the crowns of adjacent functional teeth: Absent. The maxillary teeth are closely packed, but present an almost rectangular form in lateral view which eliminates the spaces between the crowns of adjacent functional teeth without leaving any space left over for the replacement crowns (Fig. 8A). No replacement crowns are visible in the maxillary series in either specimen, although only a small part of the series is visible in the 'Dunluce' skull. The dentary toothrows do show replacement crowns filling in the gaps between the bases of adjacent crowns, and have much more the standard appearance of ornithopod toothrows.

Prominent primary ridge on the lateral side of the maxillary crown: Absent. Although, as mentioned above, there are primary ridges on the lateral faces of the maxillary crowns, they are not prominent. And, due to their placement, they are almost impossible to discern in lateral view in the type, and can most easily be made out in cross section where the maxillary teeth have been broken.

Ornamentation of apical margin of individual denticles: Absent, no denticles show any indication of ornament.

Cervical neural spines very weak or absent: Absent. The cervical series has yet to be completely prepared, but the neural spines seem to be well-developed.

Robust, arching cervical postzygapophyses posterior to axis: Present. Such postzygapophyses are present at least in the anterior postaxial cervical series.

Moderate opisthocoely in cervical vertebrae 4-9; slight opisthocoely in dorsal vertebrae 1-2: Absent. The dorsals, having been found disarticulated and rather broken, have so far resisted efforts at determining their position. The anterior cervicals show moderate opisthocoely, but a posterior centrum is only slightly opisthocoelous.

Only one of these character states (or one and a half, being liberal about the first state) of six determinable (out of a total of nine) match those

FIG. 11. Left femur of *M. langdoni* (QM F6140) in A, posterior; and B, anterior views. A block of matrix (bar) still adheres to the proximal surface of the neck. Scale = 200mm.

of ankylopellecians, thus *Muttaburrasaurus* seems not to be an ankylopellecian, contrary to the view of Bartholomai & Molnar (1981).

STYRACOSTERNA

At least 25 vertical columns in maxillary and dentary tooth rows: Absent. Eighteen columns are visible in place in the type skull. If the portion of the maxilla anterior to the anteriormost preserved tooth also held teeth there is space to accomodate at most only three additional columns. The back of the maxilla could accommodate one, or at most two, teeth, making the maximum estimate of maxillary columns 23. There are 22 on the right side in the 'Dunluce' skull.

Lanceolate-shaped maxillary crowns: Absent (Fig. 8A, B, E, F).

Strong opisthocoely in cervical vertebrae, beginning with the third cervical: Absent. The cervicals are opisthocoelous, but only weakly.

Humerus with proximally and posteriorly prominent head: Present. The right humerus of the type has a prominent, posteriorly-projected head.

Distal end of prepubic process moderately expanded dorsoventrally: Present? This was believed to have been present by Bartholomai & Molnar (1981), and cannot presently be re-assessed.

Pubis with distinct, stout iliac peduncle: Absent. The proximal piece of pubis is abraded, but the form and orientation of the acetabular region suggests that a distinct iliac peduncle was not present (Fig. 12).

Femur with deep anterior intercondylar groove: Present, as discussed above (Fig. 11B).

Two or three of the determinable seven character states (out of 12 total) are present, which suggests that *Muttaburrasaurus* is not a styracosternan.

IGUANODONTOIDEA

External nares enlarged: Absent. Although the rostrum is missing from both skulls, the portions of the narial regions preserved give no indication that the nares were enlarged. The 'Dunluce' skull, although crushed in this region, suggests that the nares were slit-like and restricted to the anterior and dorsal faces of the nasal bulla. The type skull is less forthcoming, but shows no evidence contradicting this. In *Iguanodon* and hadrosaurs the naris is noticeably enlarged. There is no indication of similar enlargement in *Muttaburrasaurus*.

At least slight transverse narrowing of cranium from postorbital region, dorsal view: Absent. Molnar (1995) showed this is clearly not the case.

Paroccipital process relatively broader proximally and narrower distally: Absent. This is also not the case in *Muttaburrasaurus*, with the paroccipital process being broad (dorsoventrally) distally. The distal extremity of the process is missing, but the posterior face of the quadrate is nearly complete. It indicates that the distal end of the paroccipital process was not declined as in *Iguanodon*.

Manual digit V with at least three phalanges: Present. If the manual digits were correctly interpreted by Bartholomai & Molnar (1981), then manual digit V has at least three phalanges.

The one out of four determinable states (from a total of 12) indicates that *Muttaburrasaurus* is not an iguanodontoid.

On the basis of what is known about *Muttaburrasaurus* it cannot be accommodated in any node distal to that of Ornithopoda, and even that is not as secure as might be wished. Presumably it is a genasaur, but may represent a lineage that

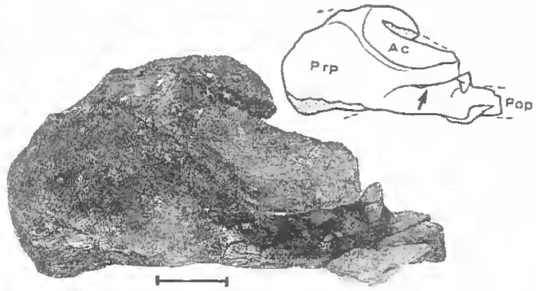

FIG. 12. Left (incomplete) pubis of *M. langdoni* (QM F6140). Arrow indicates pubic notch. Ac= acetabulum, Pop=postpubic process, Prp=prepubic process. Scale = 50mm.

diverged from the iguanodont-hadrosaur line prior to the divergence of *Tenontosaurus*.

PALAEOBIOLOGICAL SPECULATIONS

The type skull and that from 'Dunluce' differ in unexpected ways, specifically in maxillary tooth form and, apparently, the structure of the nasal bulla. There may be other differences, regarding the form of the jugal-maxillary contact (Fig. 7) and absence of replacement crowns in the maxillary series, but the state of preservation and preparation makes these uncertain. Therefore the question naturally arises as to the significance of the differences. This is also linked to the differences of the isolated maxillary teeth from Lightning Ridge. The differences may be interpreted in several fashions, as: stages in evolution; samples of population variation; examples of sexual dimorphism; stages of growth. I see no reason to regard them as pathological variants.

The two skulls may simply represent variant individuals, but if so the differences in the nasal bulla imply considerable variation in this structure. Because of this, skulls discovered in the future would be expected to also vary in structure from those now known. Although admittedly not calculable, the likelihood of finding by chance two extreme variants in bullar, and dental, structure would seem small. The uniformity of maxillary tooth form in the type skull argues against the difference from the 'Dunluce' specimen being due to variation in form along the toothrow. Growth seems an inappropriate explanation for differences between two skulls of almost equal size. It may, nonetheless, be relevant to the teeth from Lightning Ridge, which are smaller than those in the Queensland skulls. However, those teeth also differ in form from those of both skulls.

Changes in tooth form with ontogeny have never been systematically described in ornithischians, despite having good ontogenetic series of ceratopians (Brown & Schlaikjer, 1940; Dodson, 1976) and hadrosaurs (Dodson, 1975). Some of the recently discovered embryonic or hatchling dinosaur material have no teeth suitable for comparison with mature teeth (Carpenter, 1994; Chure et al., 1994) but some do. In the absence of systematic studies, the differences will be summarised here. Jacobs et al. (1994) figure a juvenile ankylosaur tooth that seems not to differ significantly from adult teeth. Since the specimen was not referred to a known taxon appropriate adult teeth for comparison are not available, so this is a tentative conclusion. Carpenter (1982) and Hatcher et al. (1907) reported that teeth of juvenile ceratopians lack the bifurcated root of adult teeth. Horner and Currie (1994) describe and figure teeth of embryonic and neonatal specimens of *Hypacrosaurus stebingeri*. Unless the adult teeth, so far undescribed, are very different from all other adult hadrosaur teeth the neonatal teeth are more plesiomorphic in appearance (Horner & Currie, 1994, figs 21.4A, 21.22, 21.23). The crowns are broader, leaf-shaped, and in the maxillary teeth have a more prominent primary ridge and marginal denticles. Superficially they have more resemble iguanodontian than hadrosaurian teeth. The tooth from Lightning Ridge does not show these kinds of differences from those of the Queensland *Muttaburrasaurus*, which suggests that it is not from a juvenile.

The nasal bulla is a large, prominent, cranial structure. Such structures in hadrosaurs may well have been associated with sexual selection and sexual dimorphism (Molnar, 1977; Dodson, 1975), so this is not unlikely in *Muttaburrasaurus* as well. Even the difference in tooth form may be related. Shine (1989) points out that females, particularly during the reproductive season, may have different nutritional requirements than males. In some ducks, for example, this is reflected in the lamellar form of the bills (Shine, 1989). Although the specific differences in *Muttaburrasaurus* food requirements obviously remain unknown — as does its food in general — this is a possible explanation for the difference in tooth form.

That the differences in form may represent evolutionary changes is suggested by the differences in age of the material. The type specimen derives from the Mackunda Fm. of Late Albian age, the 'Dunluce' specimen from the underlying Allaru Mudstone also Late Albian, and the Lightning Ridge teeth from the Griman Creek

Fm., from the Middle Albian (Exon & Senior, 1976; Burger, 1986). Thus the differences may define a temporal sequence. This notion fits the changes in form of the maxillary teeth, with a progressive reduction in the prominence of the primary ridge and its progressive shift to distal edge of the lateral face. The Lightning Ridge teeth suggest a third trend, toward an increased number of secondary ridges. The presence of two possible replacement teeth in the 'Dunluce' skull and none in the type skull is consistent with a trend toward the replacement of the maxillary toothrow en masse. The adaptive — or otherwise — nature of these changes cannot now be assessed. However, the result of the trends provides an almost unbroken strip of enamel along the maxillary toothrow for the dentary dentition to operate against. (This remains true even if there is some individual replacement of the anterior maxillary teeth.) This strip would presumably be only minimally impaired during the en masse replacement of the maxillary teeth. This is consistent with an adaptive change in the toothrow to give, or improve, a shearing function.

Thus of the five potential explanations for the differences considered here two, pathology and ontogentic development, are rejected. The remaining three, variation, sexual dimorphism and phylogenetic trends, remain viable alternatives. If the evolutionary trends are real — and they are based on only a few specimens — it should be possible to find an ancestral form that is consistent with them. As I (Molnar, 1991, 1992) have argued that the Australian dinosaur fauna was partially isolated from those elsewhere, such a form should be available in Australia. The only other Australian ornithopods are those from Lightning Ridge (New South Wales) described by Molnar & Galton (1986) and those from southern Victoria described by Rich & Rich (1989). A tooth from Lightning Ridge (QM F9505, a cast), mentioned by Molnar (1984), shows no particular resemblanee to those of *Muttaburrasaurus*, nor do the maxillary teeth of *Leaellynasaura amicagraphica* (Rich & Rich, 1989, fig. 3A). Those of *Atlascopcosaurus loadsi* (NMV P157390, referred) from the Eumeralla Fm. (deposited near the Aptian-Albian boundary) do show a prominent primary ridge, arising from the base of distal margin of the crown. A literature survey of the teeth of other small or plesiomorphic ornithopods (*Camptosaurus, Dryosaurus*, fabrosaurs, *Hypsilophodon, Kangnasaurus, Parksosaurus, Tenontosaurus, Thescelosaurus, Yandusaurus, Zephyrosaurus*) shows nothing matching the maxillary teeth of *Atlascopcosaurus*, althougsome of those of *Yandusaurus hongheensis* (He, 1979) show a primary ridge displaced toward the distal margin.

The maxillary teeth of *Atlascopcosaurus* provide a possible plesiomorphic form of the teeth of the *Muttaburrasaurus* lineage, and a link to the form of teeth in overseas ornithopods, such as *Yandusaurus*. This is consistent with the greater age of *Atlascopcosaurus*, and provides some evidence that the differences do represent evolutionary trends rather than sexual dimorphism or simple variation. Nonetheless the sample size of specimens is so small that these other potential explanations should not be completely ruled out.

CONCLUSIONS

Examination of the holotype (QM F6140) and a second specimen (QM F14921) of *Muttaburrasaurus* indicates that it cannot be referred to the Hypsilophodontia, Iguanodontia, Ankylopollexia or more distal nodes of the iguanodontian lineage as defined by Sereno (1986). It may represent a lineage that diverged from this line before the divergence of *Tenontosaurus*.

Differences in bullar structure and dental form suggest that QM F14921, from the Allaru Mudstone, is slightly more primitive than the type specimen of *Muttaburrasaurus langdoni*, from the younger, Late Albian Mackunda Fm. Variation and sexual dimorphism are deemed possible, but less likely, explanations. This material, together with a tooth from the Griman Creek Fm. at Lightning Ridge, suggests that the teeth in this lineage evolved to progressively reduce the size of the primary ridge on the maxillary teeth, progressively displace it towards the posterior (distal) edge of the lateral face and increase the number of secondary ridges. This provided a continuous, lightly corrugated strip of enamel along the lateral side of the upper dentition. This condition is consistent with the earlier (Bartholomai & Molnar, 1980) suggestion of a shearing dentition in *Muttaburrasaurus*. The maxillary teeth of *Atlascopcosaurus* (NMV P157390) are close to the expected ancestral state of those of *Muttaburrasaurus*.

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